THE CAMPANIAN TERLINGUA LOCAL FAUNA, WITH A SUMMARY OF OTHER VERTEBRATES FROM THE AGUJA FORMATION, TRANS-PECOS TEXAS

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ABSTRACT—The Terlingua local fauna is a rich assemblage of predominantly terrestrial microvertebrates from the Upper Cretaceous Aguja Formation of Trans-Pecos Texas. Marine invertebrates (which include elements of both Cretaceous Western Interior and Gulf Coast zoogeographic provinces) from conformably underlying strata suggest that the fauna is of late Campanian age, probably correlative with Judithian assemblages of the Western Interior. A Judithian "age" for the fauna is further supported by its mammal and theropod assemblages, and by the faunas of overlying deposits. The previously reported diversity of the Aguja Formation, which we summarize, is significantly enriched by this new fauna. The fauna also fills a major gap in the biogeography of Campanian terrestrial vertebrates.

Notable occurrences in the Terlingua local fauna include the therian mammal *Gallolestes*, previously known only from Baja California, and a hitherto unrecorded type of primitive 'tribothere.' At least 4 marsupial and 6 multituberculate taxa are present, several of which represent new taxa. Squamates comprise at least 10 taxa, including xenosaurs, necrosaurs, glyptosaurines, scincids, teiids, and a snake, several of which represent new taxa. In addition, the fauna includes at least 7 dinosaurs, 1 pterosaur, 2 crocodylomorphs, 3 turtles, 3 lissamphibians, 3 actinopterygians, and 8 chondrichthyans. Wood, amber, leaves, seeds, pollen, molluscs, and dinoflagellates are also preserved. The fauna is not strictly comparable to others from the Western Interior. It includes taxa that are either endemic or otherwise known only from relatively low latitudes, indicating an appreciable degree of latitudinal differentiation among Campanian terrestrial faunas bordering the Western Interior seaway.

INTRODUCTION

The North American record of Late Cretaceous vertebrates derives mainly from the central and northern Rocky Mountain region, where a relatively complete sequence is represented for Campanian and Maastrichtian time (see Clemens et al., 1979). Thus, much of the data fueling current controversies on diversity patterns approaching the Cretaceous–Tertiary boundary is based on collections from north of what is now roughly 44° North latitude. Exceptions include Turonian through Campanian assemblages from southern Utah (Cifelli, 1990a, b, c, d, e; Cifelli and Eaton, 1987; Eaton, 1987; Eaton and Cifelli, 1988), Campanian and Maastrichtian faunas from the San Juan Basin, New Mexico (Armstrong-Ziegler, 1978, 1980; Clemens, 1973; Flynn, 1986; Rigby and Wolberg, 1987; Sullivan, 1981; Wolberg and LeMone, 1979), a small Campanian fauna from Baja California (Lillegraven, 1972, 1976; Morris, 1973), and several isolated occurrences (e.g., Krause and Baird, 1979).

We report here on a predominantly terrestrial fauna from a rich microvertebrate locality in the Upper Cretaceous Aguja Formation of the Big Bend region of Trans-Pecos Texas (Fig. 1). This area lies at approximately 29° North latitude and includes terrestrial sediments which record the Cretaceous–Tertiary boundary, and which have produced a diverse but as yet poorly known fauna. The Big Bend region is uniquely situated between the Cretaceous Western Interior and Gulf Coast zoogeographic provinces, and contains elements of both. The faunas of the Aguja and stratigraphically adjacent formations occupy a pivotal position in correlating biostratigraphic zonations developed for each province, and may eventually document Late Cretaceous faunal interchange between North and South America.

The microvertebrate assemblage discussed below rivals in diversity the well known Late Cretaceous faunas of Alberta, Wyoming, and Montana, and it adds substantially to the documented biotic diversity of the Aguja Formation as a whole. The locality has yielded the first Campanian therian mammals and squamates from Texas, and, when more thoroughly studied, we expect to name new species in these groups, and perhaps in others. The locality also produced wood, leaves, pollens, spores, molluscs, and dinoflagellates. The fauna is considerably richer than other southern faunas, such as that of the "El Gallo Formation" of Baja California (e.g., Lillegraven, 1976; Morris, 1973), and it exceeds the diversity of the 'Hunter Wash,' 'Fossil Forest,' and other local faunas of the Fruitland-Kirtland formations of the San Juan Basin (Clemens, 1973; Armstrong-Ziegler, 1978, 1980; Flynn, 1986; Rigby

and Wolberg, 1987). Because investigations are continuing and we expect that representation of most taxa will be greatly improved in the near future, we have refrained from naming new taxa, although several could be diagnosed on the basis of materials now in hand.

We refer to the fauna from the microvertebrate locality informally as the "Terlingua local fauna." The Aguja Formation includes both marine and terrestrial deposits, and it represents a considerable duration of Late Cretaceous time. Designating a local fauna avoids mixing references to non-comparable environments and significantly different time planes, and may aid the development of a biostratigraphic framework offering fine levels of stratigraphic resolution within the Aguja Formation. Because little has been mentioned in the literature of the many other important vertebrate fossils previously recovered from the Aguja Formation, we also present an uncritical summary of the approximately 70 vertebrate taxa from the Aguja Formation that have been reported in unpublished dissertations and theses (Davies, 1983; Lawson, 1972; Lehman, 1982, 1985a; Standhardt 1986), and elsewhere (e.g., Russell, 1988; Langston et al., 1989; Weishampel, 1990).

Data summarized below indicate that the Terlingua local fauna is temporally correlative with Judithian assemblages of the Western Interior. Though not yet adequately studied, it is evident that the Terlingua local fauna is not merely a southern extension of a more northerly Campanian fauna. It contains a number of distinctive elements that are either endemic or are restricted to this and other southern faunas.

Abbreviations for institutions cited in the text: OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; TMM, Texas Memorial Museum, Vertebrate Paleontology and Radiocarbon Laboratory, University of Texas, Austin, Texas.

GEOLOGICAL OVERVIEW

The Aguja Formation comprises an eastward-thinning series of paralic and marine sandstones interbedded with shale and lignite deposited in a coastal plain environment. Two progradational cycles are represented in these deposits, the lower of which is present only in the western Big Bend region. Lehman (1985a, b, 1986, 1989) informally divided the Aguja Formation into several members (Fig. 2). The basal sandstone member is a progradational deltaic sandstone. It is overlain by the lower shale member, which consists of interbedded carbonaceous shale and lignite that accumulated in coastal marshes and swamps landward of the shoreline. A thin transgressive marine sandstone, the Rattlesnake Mountain sandstone member, overlies the lower shale and was deposited in a shallow marine shelf environment. A thin marine shale overlies the Rattlesnake Mountain sandstone. This shale is a westward-thinning tongue of the Pen Formation interposed within the Aguja, and is informally referred to as the McKinney Springs tongue. Overlying this
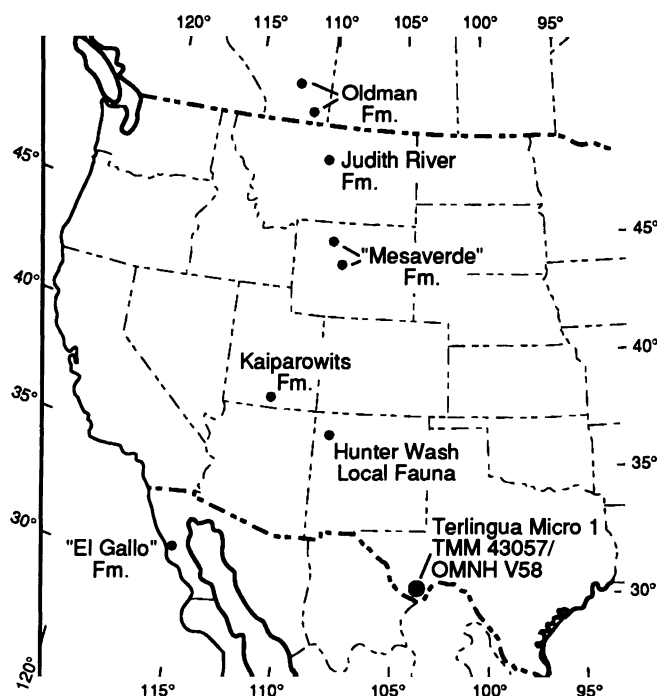

FIGURE 1. Map of western North America showing the approximate locations of Judithian terrestrial vertebrate faunas.

marine shale is a second progradational deltaic sandstone, the Terlingua Creek sandstone member, which is extensive over the entire Big Bend region. Paleocurrent data indicate that this unit prograded eastward across this region, and that the paleo-shoreline trended roughly north-south (Lehman, 1985a, b, 1986). Overlying the Terlingua Creek sandstone is the upper shale member of the Aguja Formation. This unit consists of mudstone, carbonaceous shale, lignite, and lenticular sandstone deposited in coastal swamps and marshes, and in succeeding fluvial environments, landward of the advancing shoreline. Fluvial deposits of the Upper Cretaceous Javelina Formation gradationally overlie the upper shale member of the Aguja Formation, followed by a thick sequence of terrestrial Tertiary sedimentary rocks (e.g., Maxwell et al., 1967; Schiebout, 1974; Stevens et al., 1969, 1984; Wilson, 1977, 1984, 1986; Wilson et al., 1968).

FOSSIL RECOVERY METHODS

Recovery methods used at the site yielding the Terlingua local fauna are standard for microvertebrate collecting. Rock matrix was quarried at the locality, broken into golfball- to baseball-sized chunks, and removed from the site by hand. The matrix was processed by underwater sieving (e.g., McKenna, 1965), using fine-meshed (0.30 mm) screens. Although use of fine screens prolongs processing, the recovery of extremely small teeth, which otherwise would have been lost, justifies the extra investment in labor. Because the washed con-
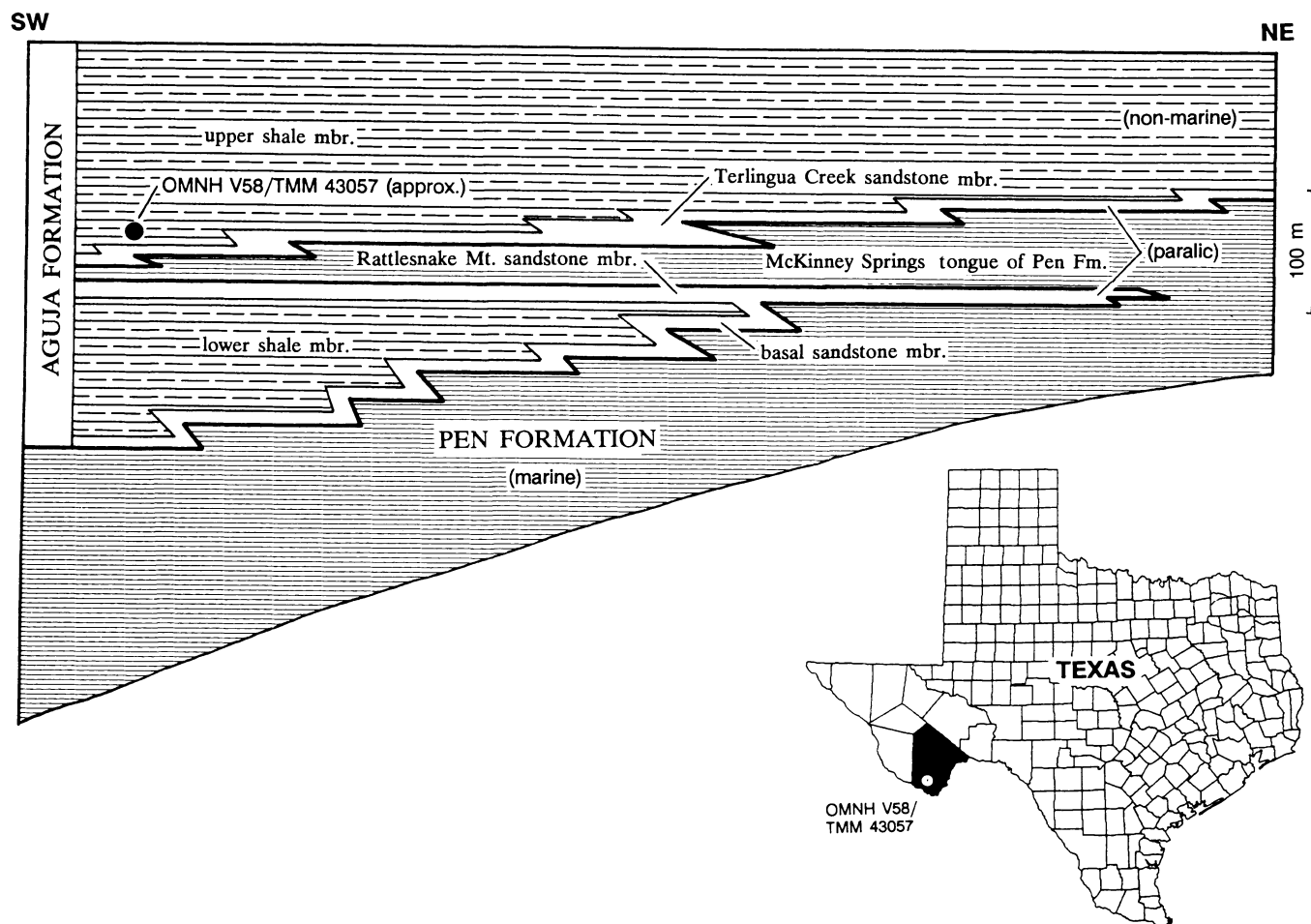
FIGURE 2. Stratigraphic relationships of the Pen and Aguja formations through Big Bend National Park, including informal units designated by Lehman (1985a, 1989). The shaded area of the map, including the approximate location of the microsite, is Brewster County, Texas.

centrate contained abundant residual carbon, the samples were subsequently separated with the heavy liquid zinc bromide (e.g., Reynolds, 1983), adjusted to a specific gravity of between 2.3 and 2.4, prior to picking concentrate under a dissecting microscope. Processing of samples collected in 1988 yielded approximately 17 mammal specimens per 100 kg of original rock matrix, a high level of productivity by Cretaceous standards.

THE TERLINGUA LOCAL FAUNA LOCALITY

The microvertebrate locality (OMNH V58; TMM 43057) lies approximately 8 km NNE of Study Butte, Brewster County, Texas (Figs. 1, 2). Detailed locality information is on file at the Oklahoma Museum of Natural History and the Vertebrate Paleontology and Radiocarbon Laboratory of the University of Texas.

The locality is stratigraphically within the lower part of the upper shale member of the Aguja Formation, within several meters of the top of the underlying marine Terlingua Creek sandstone member (Fig. 2). The bone-producing bed rests upon a distinctive, laterally

continuous lignite that contains twigs and branches of carbonized wood, leaf material, amber, and angiosperm seeds. The microvertebrate-bearing bed is 13 to 18 cm thick, and consists of discontinuous stringers of fine (granule to small pebble) conglomerate separated by thin lenses of fine sandstone and clayey siltstone. The conglomerate stringers are the principal source of the microvertebrate fossils. Clasts in the conglomerate range up to 2 cm in diameter, although most are less than 1 cm. The clasts comprise clay balls, wood, coal, amber, coprolites, and abundant, disarticulated microvertebrate bones and teeth. The site also produces isolated larger bones, most notably isolated limb elements and vertebrae of a hadrosaur, and shell fragments of a huge trionychid turtle. Many bones in all size classes are broken. Some bones exhibit varying degrees of abrasion and rounded edges indicative of transport before burial. Branches of carbonized wood lacking preferred orientation are common at the top of the bone-producing horizon. Most of this wood contains mud filled *Teredolites* (shipworm) borings.

The bone-bearing deposit ranges up to 10 m wide,

and represents deposition in a shallow channel with a sluggish current. Downcutting into the underlying lignite was not observed at the locality itself, but it does occur in similar, adjacent deposits at the same stratigraphic level. Overlying the channel are overbank deposits of clay-rich siltstone, typical of Lehman's (1985a) coastal floodplain facies.

Both the geology and faunal composition (see below) indicate a predominantly terrestrial source for the sediment and fossils preserved at the site. However, there is also evidence of significant marine influence on the faunal composition, which is not surprising given the stratigraphic proximity of marine sediments. *Teredolites* indicates a brackish or saline environment, and relatively direct communication to an open marine environment. There are eight sharks in the fauna (see below) that further support this interpretation, in that all eight taxa have also been recovered from marine sediments. Lepisosteids and amiids, also well represented in the fauna, are primarily freshwater taxa although both have high salinity tolerances and are consistent with an estuarine environment (Hoese and Moore, 1977; Bryant, 1987).

VERTEBRATE COLLECTIONS FROM THE AGUJA FORMATION

Significant collections from the Aguja Formation were first made between 1938 and 1940 under the direction of William Strain (University of Texas at El Paso), who directed a Works Progress Administration paleontological project in west Texas. At nearly the same time, collections were made by Barnum Brown for the American Museum of Natural History, and by William McAnulty, Donald Savage, and Wann Langston, Jr., for the University of Oklahoma (for details see Lehman, 1985a, 1989; Langston et al., 1989; Davies and Lehman, 1989). From the 1960s through the 1980s, Dr. Langston assembled a large collection of Aguja vertebrates for the Vertebrate Paleontology Laboratory of the University of Texas, an effort carried on by some of his students (e.g., Davies, 1983; Lehman, 1982, 1985a, 1989). Most of this work focused on the megafauna, but a recent collaborative effort by the University of Oklahoma and University of Texas collected a large sample of Aguja microvertebrates that significantly increased the documented diversity of Aguja vertebrates (Cifelli and Rowe, 1990). Judith Schiebout and Barbara Standhardt of Louisiana State University made additional microvertebrate collections in the 1970s and early 1980s. The net result of these 50 years of collecting in the Aguja is more than 1,000 cataloged specimens representing roughly 70 vertebrate species.

Although Aguja vertebrates have been known for more than half a century, few Aguja taxa have received comprehensive treatment in the literature. The first descriptions of these materials were by Brown (1942), followed by Colbert and Bird (1954) on the giant crocodilian *Deinosuchus* (=Phobosuchus) *riograndensis.* Apart from the description of a shark by McNulty and

Slaughter (1972), only some of the Aguja archosaurs were subsequently described (Coombs, 1978; Davies, 1983; Lehman, 1982, 1985a, 1989). Much of the work carried out by Louisiana State University in the Aguja Formation was summarized in a dissertation (Standhardt, 1986), but apart from a faunal summary tabulated by Standhardt (*in* Langston et al., 1989), none of this work is published.

THE TERLINGUA LOCAL FAUNA

Below is a list of taxa comprising the Terlingua local fauna, and a brief discussion of its major components. We adopted a conservative approach in taxon identification, taking names only to the levels permitted by material recovered from this locality. For example, although isolated ceratopsian teeth recovered from the locality probably represent *Chasmosaurus mariscalensis,* named from material collected elsewhere in the Aguja (Lehman, 1982, 1989, 1990a), we prefer to assign them to Ceratopsidae until more specifically diagnostic material is identified in collections from the site. We also note that many identifications are based more on phenetic resemblances than on the presence of demonstrable synapomorphies, because phylogenetic analyses at alpha levels are not yet available for most of the taxa at issue. Thus, many of the names used below could be thought of as "form taxa" rather than monophyletic entities. The major exception to this is in our discussion of the squamates, which benefits from the phylogenetic hypotheses developed by Estes (1983b), Estes et al. (1988), Gauthier (1982) and Gauthier et al. (1988). Taxa marked with an asterisk (*) represent first occurrences for the Aguja Formation. Voucher specimens are listed in Appendix 1 for all taxa discussed below.

CHONDRICHTHYES
  Euselachii
    Hybodontoidea
      Hybodontidae
        Hybodus sp.
      Hybodontidae, indet.
      Polyacrodontidae
        Lissodus (=Lonchidion) *selachos*
    Lamniformes
      Mitsukurinidae
        Scapanorhynchys sp.
  Batomorphii
    Rajiformes
      Sclerorhynchidae
        Onchopristis dunklei
        Ischyrhiza avonicola
    Rajiformes incertae sedis
        Squatirhina americana
        Ptychotrygon sp.
    Batomorphii indet.
    Myliobatiformes
      Dasyatidae
  Chondrichthyes indet.

ACTINOPTERYGII
Lepisosteidae
Amiidae
Teleostei
*Phyllodontidae
Teleostei indet.
LISSAMPHIBIA
Urodela
Prosirenidae
Albanerpeton sp.
Scapherpetontidae
Urodela indet.
*Anura
CHELONIA
Cryptodira
Trionychidae
"*Aspideretes*"
Baenidae
"*Baena*"
Chelonia indet.
SQUAMATA
*Anguimorpha
*Anguidae
*Glyptosaurinae
* *Odaxosaurus* sp.
* *Proxestops* sp.
Glyptosaurinae indet.
Anguidae indet.
*Xenosauridae
Restes sp.
Varanoidea
*Necrosauridae
*Scincomorpha
*Scincidae
**Sauriscus* sp.
*Scincidae sp. nov. A.
*Teiidae
*Teiidae sp. nov. B
*Serpentes
Squamata indet.
*Squamata sp. nov. X
*Squamata sp. nov. Y
CROCODYLIA
Mesosuchia
Goniopholidae
Eusuchia
Deinosuchus riograndensis
*PTEROSAURIA
DINOSAURIA
Ornithischia
Ankylosauria
Ornithopoda
Hadrosauridae
Ceratopsia
Ceratopsidae
Saurischia
Theropoda
Carnosauria
Tyrannosauridae

Maniraptora
Troodontinae
*cf. *Troodon*
Velociraptorinae
*cf. *Saurornitholestes*
Dromaeosaurinae
*cf. *Dromaeosaurus*
Maniraptora incertae sedis
*cf. *Ricardoestesia*
MAMMALIA
Multituberculata
*Neoplagiaulacidae
Cimolomyidae
**Cimolomys clarki*
Meniscoessus
**Meniscoessus* sp. nov.
*Cimolodontidae
**Cimolodon* cf. *electus*
*cf. *Cimolodon*
Multituberculata incertae sedis
gen. et sp. nov.
Marsupialia
*"Peradectidae"
**Alphadon* cf. *A. wilsoni*
**Alphadon* sp. nov.
**Turgidodon* sp.
Pediomyidae
**Pediomys* cf. *P. krejcii*
?Eutheria
**Gallolestes* sp.
Mammalia, incertae sedis ("metatherian-eutherian grade" or "Tribotheria")
*sp. nov.

Chondrichthyes

For convenience, we use the nomenclature of Cappetta (1987) for chondrichthyans, though we note that the monophyly of most of the categories recognized below is not demonstrated. Eight chondrichthyan species were identified in the Terlingua local fauna (Fig. 3). Five are batoids, represented by abundant isolated teeth, occasional denticles, and rostral spine fragments. These include two sclerorhynchid rajiforms, *Onchopristis dunklei* McNulty and Slaughter (1962) and *Ischyrhiza avonicola* Estes (1964), and two rajiforms of uncertain affinities, *Squatirhina americana* Estes (1964) and what may be a new species of *Ptychotrygon* (Fig. 3). The occurrence of *Onchopristis dunklei* is a range extension, being previously known no higher in stratigraphic position than the Cenomanian Woodbine Formation (McNulty and Slaughter, 1962; Slaughter and Steiner, 1968). Cappetta (1987) noted with skepticism reports of *Onchopristis dunklei* from the Upper Cretaceous (Campanian or Maastrichtian) of New Zealand and India.

The fifth batoid is an indeterminate dasyatid, represented by a single, large square tooth. Several fragmentary teeth in our collection may represent addi-
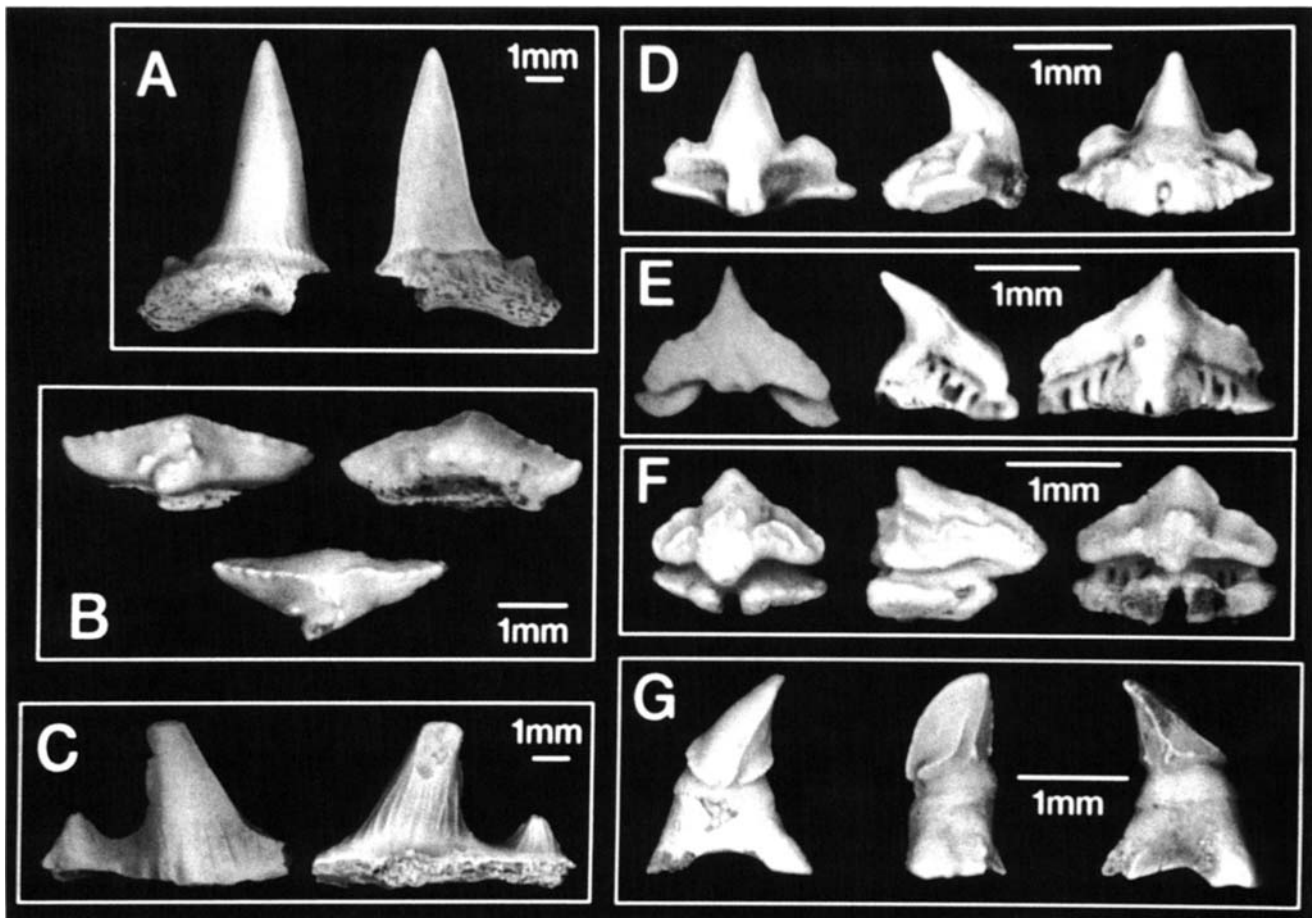
FIGURE 3. Chondrichthyans of the Terlingua local fauna. **A**, *Scapanorhynchus* sp. (TMM 43057-301) in lingual and labial views. **B**, *Lissodus* sp. (TMM 43057-302), tooth crown in labial, occlusal, and lingual views. **C**, *Hybodus* sp. (TMM 43057-321) in labial and lingual views. **D**, *Onchopristis dunklei* (TMM 43057-305) tooth in labial, mesial, and lingual views. **E**, *Squatirhina americana* (TMM 43057-297) in labial, mesial, and lingual views. **F**, *Ptychotrygon* sp. (TMM 43057-304) in labial, mesial, and lingual views. **G**, *Ischyrhiza avonicola* (TMM 43057-306) tooth in labial, mesial, and lingual views.

tional batoid taxa, but none is assignable to *Myledaphus,* a taxon common in the Fruitland-Kirtland faunas of the San Juan Basin (Armstrong-Ziegler, 1978, 1980; Wolberg and LeMone, 1979) and more northern faunas (e.g., Estes, 1964; Langston, 1975, 1976; Brinkman, 1990).

Two of the remaining chondrichthyans are hybodontid sharks. *Hybodus* sp. (Fig. 3) is represented by abundant broken teeth, and probably also by the common fragments of hybodontoid cephalic and fin spines present at the site. The second hybodontoid is *Lissodus* (=*Lonchidion*) *selachos* (Estes, 1964), which is represented by several hundred isolated teeth (Fig. 3), many of which retain their bony bases. The final shark is a lamniform, *Scapanorhynchus* sp., represented by rare, broken but unabraded teeth. A number of unidentifiable chondrichthyan vertebrae and a few badly abraded teeth were also recovered. None of the chondrichthyans is sufficiently constrained temporally to provide useful information regarding the age of the Terlingua local fauna.

Actinopterygii

Actinopterygian remains are abundant in the Terlingua local fauna. All are disarticulated and most are difficult to identify. The distinctive scales and teeth of an indeterminate lepisosteid are common, and isolated vertebrae and skull fragments are present as well. Also present are vertebrae and teeth of an indeterminate amiid. The amiid *Melvius* is reported elsewhere in the Aguja (Boreske, 1974; Bryant, 1987). Numerous small, spheroidal teeth of phyllodontid teleosts are also recognizable components of the Terlingua material. It is likely that a greater diversity of teleosts is represented in the material now at hand, which includes hundreds of tiny isolated bones. The actinopterygians, though potentially interesting, offer no useful information on the correlation and age of the Terlingua local fauna.

Lissamphibia

Both frogs and salamanders are present in the Terlingua local fauna. There are at least two salamander

species, of which the prosirenian *Albanerpeton* sp. (=*Prodesmodon copei,* in part, of Estes, 1964; see Estes, 1981) is the most abundant, being represented by more than 100 maxilla and dentary fragments. *Albanerpeton* is easily recognized by its non-pedicillate teeth and by a complex, interdigitating joint at the dentary symphysis (Estes, 1981). A wide size range of these elements is present in the large sample of jaws from Terlingua. The largest specimens are more than twice the size of the smallest specimens. Whether this is the manifestation of ontogenetic or taxonomic diversity is not yet known. A second salamander, probably a scapherpetonid, is represented by isolated vertebral elements. This may be the taxon that Standhardt (1986) identified from elsewhere in the Aguja as *Scapherpeton tectum.* Anurans, rare elements in the fauna, are represented by jaw fragments, distal ends of humeri, and partial ilia. The number and identity of the anuran taxa remain to be determined.

Albanerpeton, which ranges from the Middle Jurassic to the Middle Miocene (Estes, 1981), is uninformative regarding the age of the Terlingua local fauna. Without more specific identification, none of the lissamphibians is helpful in this respect.

Chelonia

Seven turtle taxa are reported from the Aguja Formation (Table 1), but only two were identified in the Terlingua local fauna. A large trionychid referable to the form genus "*Aspideretes*" is represented by numerous large shell fragments. The rear half of a skull and possibly other shell fragments indicate the presence of a large baenid, which Hutchison (pers. comm.) assigns to the form genus "*Baena.*" We also recovered several isolated turtle dentaries that are from much smaller individuals and that may represent two or possibly three taxa. Although turtles provided significant stratigraphic resolution elsewhere in Late Cretaceous and Early Tertiary terrestrial sediments (e.g., Hutchison and Archibald, 1986), they are as yet too poorly known in the Terlingua local fauna to be informative in this regard.

Squamata

Until now, squamates were poorly represented in southerly Late Cretaceous faunas of North America (Estes, 1983a, b). Apart from a passing mention of indeterminate mosasaurs in marine facies (Maxwell et al., 1967), no squamates were previously reported in the Aguja Formation. Only four species are known in the Fruitland Formation (Armstrong-Ziegler, 1978, 1980; Sullivan, 1981), and only one is reported for the "El Gallo" Formation (Estes, 1983a). The Terlingua local fauna fills this important geographic gap with a diverse assemblage of squamates (Fig. 4). All of the material at this site is fragmentary, consisting of isolated cranial elements, jaw fragments, isolated teeth, and isolated scutes. Nevertheless, the material permits recognition of 10 taxa.

Anguimorpha—As in other Late Cretaceous and early Tertiary faunas from the Western Interior, the most common squamate elements are isolated osteoderms of glyptosaurine anguids. Also preserved are jaw fragments and isolated teeth with the characteristic square profile of *Odaxosaurus* sp. (=*Pancelosaurus piger,* in part, of Meszoely, 1970; =*Peltosaurus piger* of Estes, 1964; see Gauthier, 1982). These specimens are among the oldest known glyptosaurines; other Campanian occurrences are reported in the correlative Fruitland, Judith River, and "Mesaverde" formations (Estes, 1964, 1983a; Sullivan, 1987), and from the eastern seaboard (Denton et al., 1991). Glyptosaurines are also well known from early Tertiary deposits of Wyoming and Montana (Meszoely, 1970; Gauthier, 1982; Sullivan 1982, 1987); the group became extinct near the end of the Oligocene. Scutes referable to the glyptosaurine *Proxestops* (see Gauthier, 1982) are also present in the Terlingua local fauna, though comparatively rare.

An additional anguid is represented by three jaw fragments. The teeth in these specimens are strongly recurved or bowed posteriorly, and the crowns are striated lingually but not laterally. The crowns are bicusped, with a small anterior lobe separated from the larger posterior lobe by a groove on both the lingual and lateral surfaces. Specimens such as these were commonly assigned to Gerrhonotinae in earlier literature (e.g., Armstrong-Ziegler, 1978, 1980; Sullivan, 1981). However, Good (1988) recently argued that this tooth form is plesiomorphic for Anguidae, and that high variability among anguids in the other characters preserved in the fragmentary Terlingua material leave the specimens assignable to Anguidae, but not to a more specific level.

In addition to the three anguids, two other anguimorphis are present, though comparatively rare. One is a xenosaur, represented by a maxilla with teeth that have a weak anterior cusp that is set off from the large posterior cusp by a weak groove on the lateral surface. We refer this specimen to *Restes* (=*Exostinus*; Gauthier, 1982) sp. The second non-anguid anguimorph is provisionally referred to Necrosauridae. It is known from a few jaw fragments with pleurodont teeth that are laterally compressed and that have the characteristic infolded enamel of varanoids. All teeth are broken above their infolded bases. Several osteoderms in our collection may also represent this taxon. Both xenosaurs and necrosaurids are reported from Maastrichtian deposits elsewhere (Estes, 1983a; Sullivan, 1987); their occurrence in the Terlingua local fauna is the first report from Campanian sediments. Older anguimorphs were described by Winkler et al. (1990) from several localities in Early Cretaceous (Commanchean) sediments of Texas. None of the Terlingua anguimorphs is sufficiently constrained temporally to offer useful information on the age of the fauna.

Scincomorpha—Three scincomorphs are now known in the Terlingua local fauna. Two are referable to Scincidae (Fig. 4), extending the distribution of Scincidae into the Campanian for the first time in North Amer-
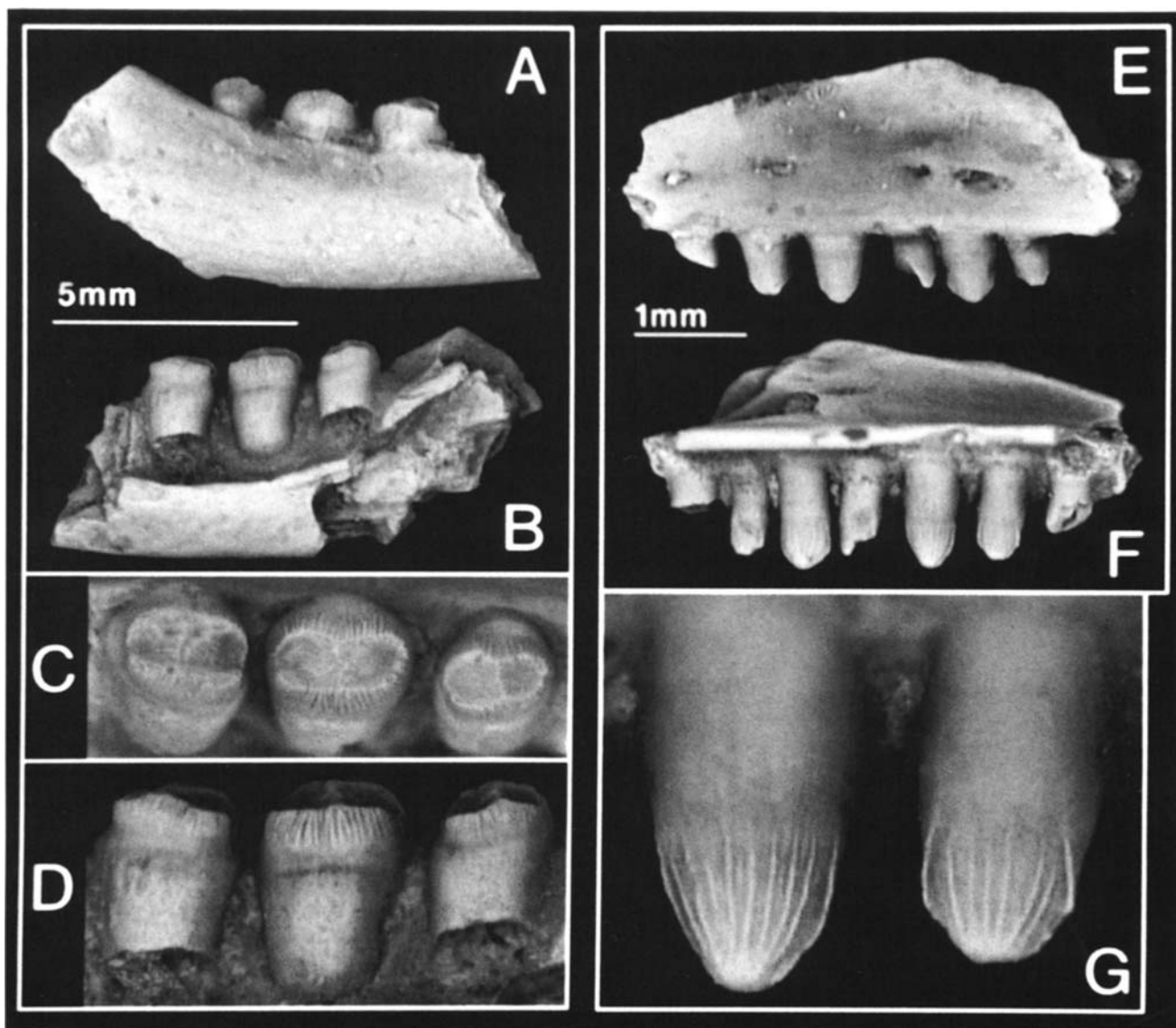
FIGURE 4. Scincids of the Terlingua local fauna. A–D, Scincidae sp. nov. (TMM 43057-286), right dentary: A, lateral view; B, lingual view; C, D, details of posterior dentary tooth crowns in occlusal and lingual views. E–G, *Sauriscus* sp. (OMNH 25347), maxilla: E, lateral view; F, medial view; G, details of tooth crowns in labial view.

ica. As Estes (1983a) and Sullivan (1987) argued, earlier reports of Campanian scincids (Russell, 1975, 1982) were in error. The most common squamate in the Terlingua local fauna, next to the glyptosaurines, is a large scincid with a highly distinctive dentition, which we refer to informally as species A. It is represented by a number of jaw fragments and isolated teeth. A peculiar feature of the dentary is that the Meckelian groove is enclosed to form a tube by fusion of the dentary along its ventral edge, from very near the symphysis posteriorly to near the level of the coronoid. The splenial is absent from the tooth-bearing portion of the mandible. The most comparable dentaries are in other scincids, although similar features also occur in dibamids, pygopodids, gekkonids, xantusiids, some gymnophthal-

mids, iguanines, and amphisbaenians, evidently arising independently in each case (Estes et al., 1988; Ethridge and de Queiroz, 1988). The teeth in the Terlingua material are similar to the large, bulbous teeth of the extant scincid, *Tiligua scincoides*. However, the Terlingua taxon is seemingly unique in that the teeth occluded to produce on each tooth a pair of crescentic wear facets, separated by a transverse ridge. Teeth lying near the front of the mouth are compressed anteroposteriorly and are considerably smaller than the more posterior, 'molariform' teeth. They also developed wear facets. In their functional arrangement and degree of heterodonty, these teeth are reminiscent of the massive dentitions of the Late Cretaceous teiid *Peneteius* (Estes, 1969), and to a lesser degree the polyglyphanodontines

TABLE 1.   Uncritical tabulation of vertebrates reported from the Aguja Formation.

Taxon	References
Chondrichthyes	
Hybodus sp.	This paper
Lissodus selachos	This paper; Standhardt, 1986
Cretorectolobus olsoni	Standhardt, 1986
Odontaspis sp.	Langston et al., 1989
Anomotodon angustidens	Lehman, 1985a
Scapanorhynchus texanus	Lehman, 1985a
Scapanorhynchus raphidon	Langston et al., 1989
Scapanorhynchus sp.	This paper; Russell, 1988
Squalicorax kaupi	Lehman, 1985a
Squalicorax sp.	Russell, 1988
Onchopristis dunklei	This paper
Onchopristis sp.	Davies, 1983; Russell, 1988
Ischyrhiza avonicola	This paper
Ischyrhiza mira	Lehman, 1985a
Squatirhina americana	This paper; Standhardt, 1986
Ptychotrygon agujaensis	McNulty and Slaughter, 1972; Langston et al., 1989; Russell, 1988
Phychotrygon sp.	This paper; Lehman, 1985a; Standhardt, 1986
Myledaphus bipartitus	Standhardt, 1986
Dasyatidae sp.	This paper
Psuedocorax (*=Corax*) sp.	Wixson, 1963
Isurus sp.	Wixson, 1963
Lamna appendiculata	Langston et al., 1989
Cretolamna sp.	Russell, 1988
Actinopterygii	
Melvius thomasi	Boreske, 1974
cf. *Melvius*	Bryant, 1987; Russell, 1988
Amiidae	This paper; Lehman, 1985a; Standhardt, 1986
Lepisosteidae	This paper; Davies, 1983; Lehman, 1985a; Standhardt, 1986
Lepisosteus sp.	Russell, 1988
Atractosteus sp.	Standhardt, 1986
Lissamphibia	
Albanerpeton	This paper
Albanerpeton nexosus	Standhardt, 1986
Scapherpetontidae indet.	This paper
Scapherpeton tectum	Standhardt, 1986
Anura sp.	This paper
Chelonia	
Adocus sp.	Lehman, 1985a; Langston et al., 1989
"*Aspideretes*"	This paper; Lehman, 1985a; Langston et al., 1989
"*Baena*" cf. *B. nodosa*	Lehman, 1985a; Langston et al., 1989
"Baena"	This paper
cf. *Basilemys* sp.	Davies, 1983; Lehman, 1985a; Langston et al., 1989
Compsemys victa	Standhardt, 1986; Langston et al., 1989
? *Taphrosphys* sp.	Lehman, 1985a; Langston et al., 1989
Thescelus cf. *T. insiliens*	Lehman, 1985a; Langston et al., 1989
Thescelus sp.	Lawson, 1972; Langston et al., 1989
Squamata	
Odaxosaurus sp.	This paper
Proxestops sp.	This paper
Restes sp.	This paper
Necrosauridae	This paper
Scincidae, sp. A	This paper
Sauriscus sp.	This paper
Teiidae, sp. B	This paper
Squamata indet., sp. X	This paper
Squamata indet., sp. Y	This paper
Serpentes	This paper

TABLE 1. *(Continued)*

Taxon	References
Mosasauridae	Maxwell et al., 1967; Lehman, 1985a; Standhardt, 1986; Langston et al., 1989
Crocodylia	
Goniopholidae	This paper
Goniopholus cf. *kirtlandicus*	Lehman, 1985a
Deinosuchus riograndensis	This paper; Colbert and Bird, 1954
cf. *Leidyosuchus*	Langston et al., 1989
cf. *Brachychampsa*	Standhardt, 1986; Langston et al., 1989
Pterosauria	
Pterosauria	This paper
Dinosauria	
Kristosaurus	
cf. *K. navajovius*	Lawson, 1972; Davies, 1983
(= ?*Gryposaurus*)	Weishampel and Horner, 1990
Hadrosauridae	This paper; Weishampel and Horner, 1990; Weishampel, 1990
Lambeosaurinae indet.	Davies, 1983; Weishampel, 1990
Hypsilophodontidae	Davies, 1983
Stegoceras sp.	Lehman, 1985a; Weishampel, 1990
Panoplosaurus sp.	Coombs, 1978; Carpenter, 1990
cf. *Euoplocephalus*	Standhardt, 1986
Nodosaurinae	Lehman, 1985a
Edmontonia cf. *rugosidens*	Coombs and Maryanska, 1990; Weishampel, 1990
cf. Ankylosauridae	Standhardt, 1986
Chasmosaurus mariscalensis	Lehman, 1989; Weishampel, 1990
Ceratopsidae	This paper; Standhardt, 1986
Tyrannosauridae	This paper; Lehman, 1985a; Weishampel, 1990
Ornithomimidae	Davies, 1983; Weishampel, 1990
Paronychodon lacustris	Standhardt, 1986; Langston et al., 1989
Troodon sp.	Standhardt, 1986
cf. *Troodon*	This paper
cf. *Saurornithoides*	This paper
cf. *Dromaeosaurus*	This paper
cf. *Ricardoestesia*	This paper
Mammalia	
"tribothere" new sp.	This paper
Ptilodontoidea	Standhardt, 1986
Eucosmodontidae	Standhardt, 1986
Cimolomyidae, new sp.	Standhardt, 1986
Meniscoessus sp.	Standhardt, 1986
Meniscoessus, sp. nov.	This paper
Cimolodon cf. *electus*	This paper
cf. *Cimolodon*	This paper
Cimolomys clarki	This paper
Neoplagiaulacidae	This paper
Multituberculata incertae sedis, sp. nov.	This paper
Alphadon cf. *A. wilsoni*	This paper
Alphadon cf. *A. marshi*	Standhardt, 1986
Alphadon sp.	This paper
Turgidodon sp.	This paper
Pediomys cf. *P. krejcii*	This paper
Gallolestes sp.	This paper

(Estes, 1983a), both of which are unknown in the Terlingua local fauna.

The second scincid is referable to *Sauriscus* sp., and is represented in the fauna by several broken jaws. Its tooth crowns bear weak striations lingually and marked striations laterally. The teeth appear somewhat different from previously described species in having crowns that are only incipiently divided into three weakly defined lobes; in other species the crowns are markedly tricusped (e.g., Estes, 1964). Both of the Terlingua scincids represent new taxa.

In addition to the two scincids, at least one teiid

occurs in the Terlingua local fauna, which we refer to informally as species B. It is represented by broken jaw fragments and isolated teeth in which there is a widely open Meckelian fossa (indicating a large splenial), extensive deposition of cementum around the bases of the teeth, and a well developed subdental shelf and sulcus dentalis (Estes et al., 1988). The Terlingua taxon differs from other Cretaceous teiids in having teeth that are weakly tricusped. The crowns are smooth laterally, weakly striated lingually, and faintly defined anterior and posterior cusps are set off from the main crown by a shallow lingual groove. Teiids have an extensive Cretaceous record in North America. Winkler et al. (1990) tentatively referred material to Teiidae from the Commanchean (Early Cretaceous) of Texas, and there is a diversity of named teiids from the Late Cretaceous. *Chamops segnis* and *Leptochamops denticulatus* are known from the correlative Fruitland Formation (Armstrong-Ziegler, 1978, 1980; Estes, 1983a; Sullivan, 1987). Kequin and Fox (1991) recently described five new teiid species in the correlative Oldman Formation, and they list eight additional Lancian teiids from North America. Like the anguimorphs, the Terlingua scincomorphs are currently of little use in refining the age of the Terlingua local fauna.

Serpentes—A snake is present in the Terlingua local fauna. One tiny jaw fragment preserves one recurved tooth that is set into a shallow socket, and on either side is an additional shallow socket. The tooth has a circular base, is strongly recurved, and lacks serrations. Armstrong-Ziegler (1978, 1980) described a snake, which she identified as an aniliid, from the Campanian Fruitland-Kirtland formations. The specimen was later identified as a boid (Rage, 1984; Estes and Báez, 1985; Sullivan, 1987). Apart from its being a snake, little can be said of the identity of the Terlingua specimen at present.

Squamata indet.—Two additional lizards, which we refer to informally as species X and species Y, are, at present, indeterminate members of Squamata. In the former, the teeth are solidly ankylosed to the jaws and their crowns are blunt and rounded. The inframandibular septum was evidently long and relatively slender. Species Y has distinctive teeth that have smooth, unicusped crowns, and there is a very narrow dental gutter. Few other details of morphology are available for either taxon at present.

Archosauria

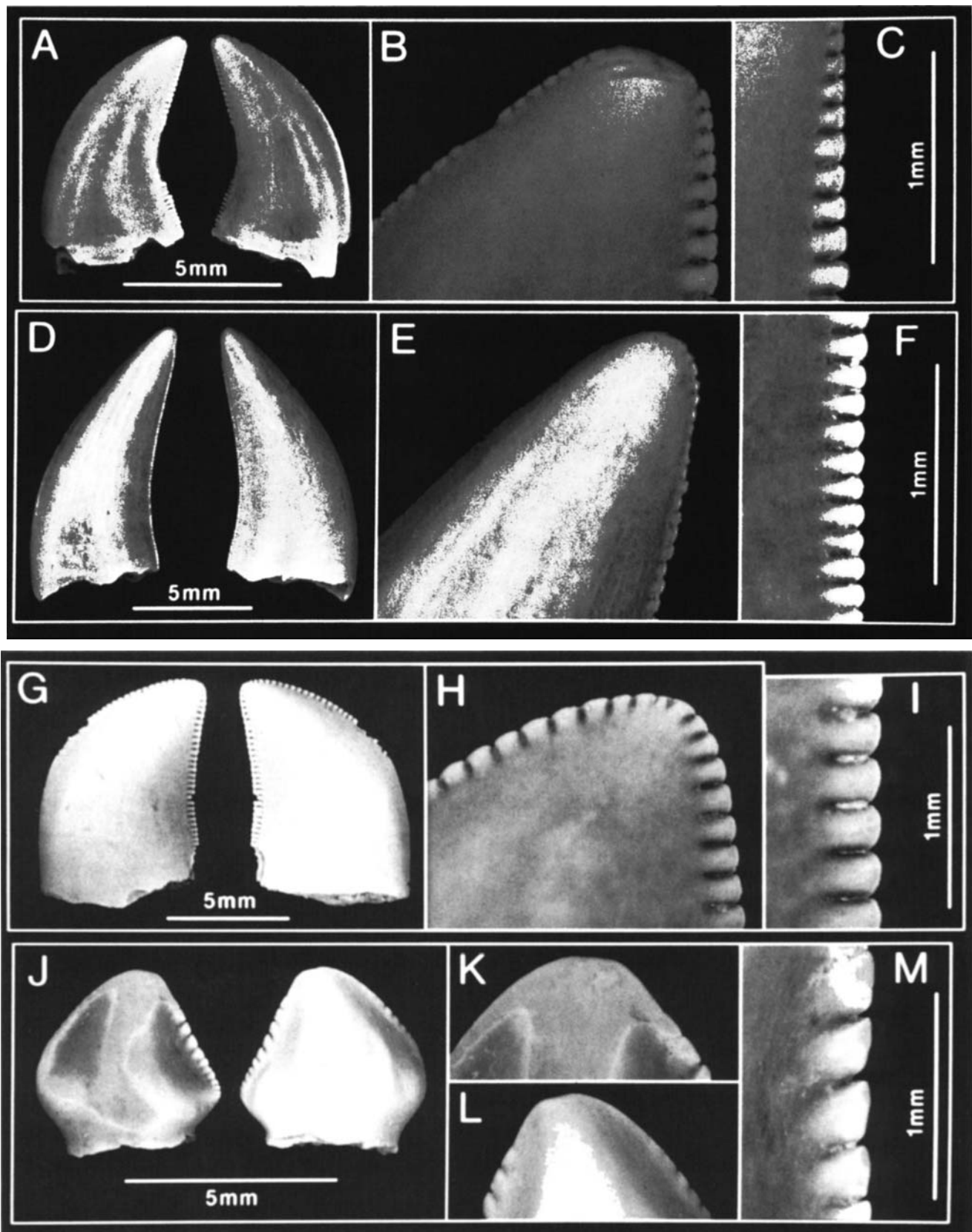**Crocodylia**—At least two crocodilians occur in the Terlingua local fauna. These are *Deinosuchus* (=*Phobosuchus*) *riograndensis* and an indeterminate goni-opholid. The Terlingua goniopholid may prove to be *Goniopholis* cf. *G. kirtlandicus*, which is known elsewhere in the Aguja (Lehman, 1985a), but available material is too fragmentary to permit more specific identification. Standhardt (*in* Langston et al., 1989) referred isolated teeth from the Aguja to *Leidyosuchus* and *Brachychampsa*, but we found no record of either in the Terlingua local fauna. We also note that Dr. Langston (pers. comm.) doubts that either taxon can be diagnosed by the fragmentary material currently known from the Aguja.

Dinosauria: Ornithischia—Three ornithischians occur in the Terlingua local fauna, the most common of which is an indeterminate hadrosaur represented by isolated teeth, ossified tendons, isolated limb elements, and vertebrae. This material includes very young and adult individuals. Both *Kritosaurus* (=?*Gryposaurus* of Weishampel and Horner, 1990) cf. *K. navajovius* (Lawson, 1972; Davies, 1983) and an indeterminate lambeosaurine (Davies, 1983; Weishampel and Horner, 1990) are reported from elsewhere in the Aguja. Ceratopsians are also present, but in less relative abundance than the hadrosaurs. *Chasmosaurus mariscalensis* (Lehman, 1989), described from material discovered elsewhere in the Aguja, is in all likelihood the Terlingua ceratopsian, but diagnostic material has yet to be recovered from the locality. The third ornithischian recorded is an ankylosaur, known only from osteoderms. None of the ornithischian remains from the Terlingua locality offers any refinement of the age of the Terlingua local fauna, although specimens from elsewhere in the Aguja support our Judithian assignment (see below).

Theropoda—Theropods are present, although only isolated teeth and a few isolated bones and bone fragments have yet been recovered. We followed the criteria described by Currie et al. (1990) in identifying isolated teeth from the Judith River Formation. The Terlingua local fauna includes at least one large tyrannosaurid, and four smaller maniraptorans (Fig. 5) which we provisionally refer to cf. *Dromaeosaurus*, cf. *Saurornitholestes*, cf. *Ricardoestesia*, and cf. *Troodon*. Standhardt (1986) identified *Paronychodon lacustris* in the upper Aguja, which may be what we refer to as cf. *Saurornitholestes* (see Currie et al., 1990). Several other teeth do not easily fit into any of those categories but generally resemble teeth of the small, bird-like theropods.

The general similarity of the Judith River theropod assemblage to that of the Terlingua local fauna may offer further corroboration of a Judithian assignment for the latter. As Currie et al. (1990) point out, however, small theropod teeth are common in most Late Cretaceous faunas, and the distributions of these recently recognized taxa are not yet well documented.

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FIGURE 5.   Small theropods of the Terlingua local fauna. A–C, Cf. *Saurornitholestes* tooth (TMM 43057-316): **A**, lateral and lingual views; **B**, detail of tip; **C**, detail of serrations along posterior edge. D–F, Cf. *Ricardoestesia* tooth (TMM 43057-313): **D**, lateral and lingual views; **E**, detail of tip; **F**, detail of serrations along posterior edge. **G–I**, Cf. *Dromaeosaurus* tooth

(TMM 43057-314): **G**, lateral and lingual views; **H**, detail of tip; **I**, detail of serrations along posterior edge. **J–M**, Cf. *Troodon* tooth (TMM 43057-323): **J**, lateral and lingual views; **K–L**, detail of tip in lateral and lingual views; **M**, detail of serrations along posterior edge.
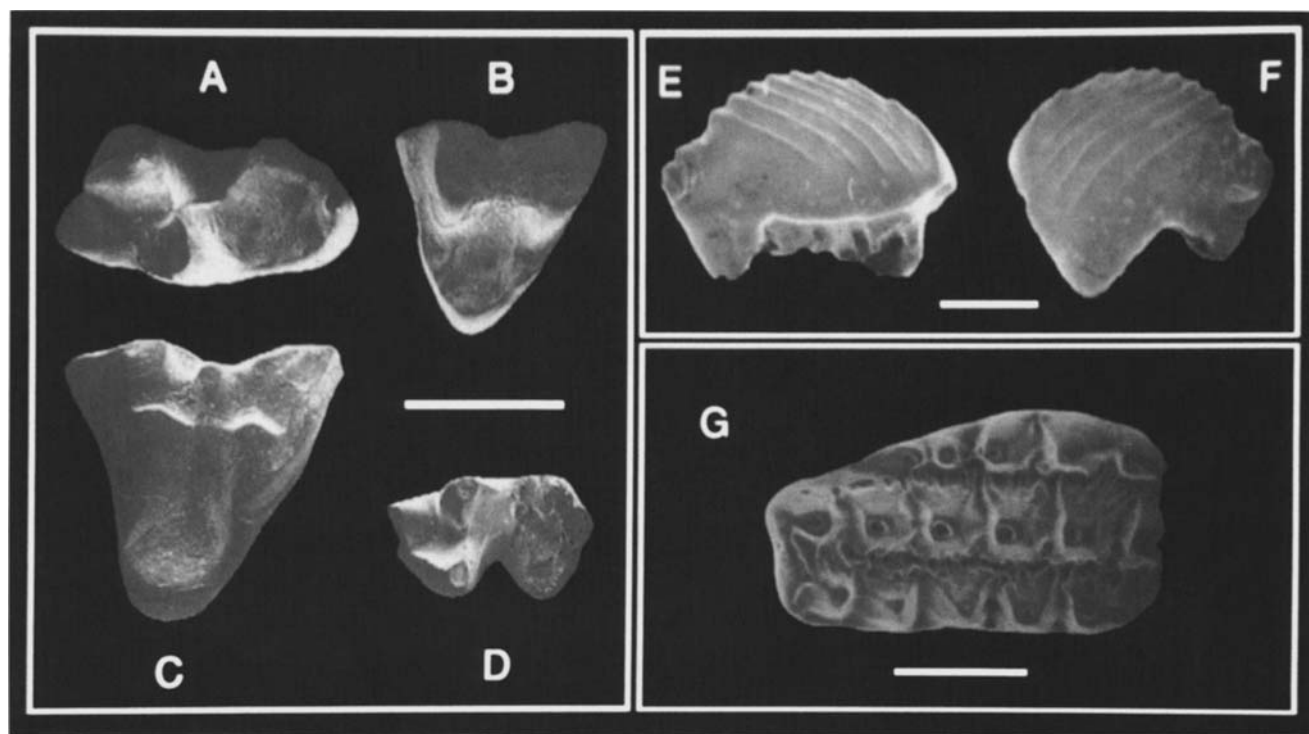
FIGURE 6. Mammals of the Terlingua local fauna. A, Tribotheria, incertae sedis, right lower molar (OMNH 22789). B, *Alphadon* sp., left upper molar (OMNH 22721). C, *Alphadon* cf. *A. wilsoni*, left upper molar (OMNH 22724). D, *Gallolestes* sp. left lower molar (OMNH 22788). E, F, *Cimolodon* cf. *electus*, left fourth lower premolar (OMNH 25042): E, lingual; F, labial. G, *Cimolomys clarki*, upper right first molar in occlusal view (OMNH 25014). A, B, C, D, and G in occlusal view; scale is 1 mm.

Pterosaurs—Several crushed, incomplete bones indicate the presence of pterosaurs in the Terlingua local fauna, although specimens now in hand are too fragmentary for more specific identification.

Mammalia

Order and Family Uncertain, gen. and sp. indet.—A presumably new taxon is represented by several lower molars. These teeth (Fig. 6) bear fully developed, tricuspid, basined talonids, and thus belonged to a tribosphenic therian in the sense of Crompton (1971). Beyond this, the affinities of the species are uncertain. Distinctive marsupial or eutherian characters are lacking, and for convenience we refer to the taxon informally as a therian of "metatherian-eutherian grade" (Patterson, 1956; Kielan-Jaworowska et al., 1979) or "tribothere" (Clemens and Lillegraven, 1986), though we recognize that neither term refers to a monophyletic unit. The species is small, with teeth slightly smaller than those of *Alphadon wilsoni* Lillegraven, 1969. The positions of the referred teeth are unknown. All specimens have rounded, posteriorly narrowing talonids, suggesting that they may be ultimate lower molars, but this may simply be a characteristic of all lower molars of the taxon. The trigonid is broadly open lingually, with the paraconid, subequal to the metaconid

in size, anteriorly placed, but not so lingual as is generally seen in marsupials (Clemens, 1979). The cristid obliqua attaches anteriorly to the base of the trigonid in a median position; a distal metacristid is lacking. The hypoconulid is in a median position, not shifted lingually as is generally true of marsupials (Clemens, 1979; Clemens and Lillegraven, 1986; Cifelli and Eaton, 1987). A labial postcingulid, also characteristic of early marsupials but seen in some Cretaceous eutherians as well (Cifelli, 1990b), is lacking.

The affinities of this taxon are puzzling. Differences in height and width of the trigonid and talonid are less pronounced than in presumably primitive Tribosphenida such as *Kermackia texana* (cf. Butler, 1978). The lack of a distal metacristid is also a derived condition within Tribosphenida (Fox, 1975), perhaps suggesting a relationship to certain "advanced" Theria of metatherian-eutherian grade, marsupials, and eutherians (Cifelli, 1990e). However, the unreduced, anteriorly placed paraconid is unlike that typical of Cretaceous Eutheria. Likewise, the median position of the paraconid, lack of a labial postcingulid, and lack of entoconid to hypoconulid twinning differ from conditions seen in early presumed marsupials or marsupial-like taxa (Cifelli, 1990c, d). An unusual tribosphenic upper molar, almost certainly too small for this species, is tentatively referred below to *Gallolestes*.

Multituberculata — Multituberculates are by far the most common mammals at the Terlingua locality, with more than 400 specimens recovered to date. The majority of these are incisors and premolars, and many of the larger teeth are fragmented. With three exceptions, the specimens are isolated teeth.

Meniscoessus is the most common multituberculate. Nine lower fourth (ultimate) premolars are now recovered, but none is intact. These show size and structural diversity that suggest the possibility of more than one taxon, though the small sample size leaves doubt on this point. Complicating identification of this material are upper and lower first molars, clearly referable to *Meniscoessus*, but which do not show divergence like that of the premolars. The Terlingua specimens most closely resemble *M. major*, but are smaller than known specimens of that taxon. We refer to these as *Meniscoessus*, sp. nov., elsewhere in this paper.

Cimolodon is known from four entire and several fragmentary lower fourth premolars. These are nearly identical in size and structure to those of *C. electus* from the Milk River Formation (Fox, 1971). Specific identification of the Terlingua *Cimolodon* is complicated, however, by the presence of upper fourth premolars that are also assignable to *Cimolodon* (Fig. 6). In most aspects of morphology they more closely resemble *C. nitidus* than *C. electus*, but they are smaller than any known specimens of *C. nitidus*. We provisionally refer to all of these teeth as *Cimolodon* cf. *electus*.

Also provisionally referred to *Cimolodon* are several molars showing an unusual, complex pattern of pitting that creates reticulated ridges on the occlusal surfaces. Teeth of *Essonodon* also share this feature, but *Essonodon* has a more regular pattern of occlusal pits and ridges, and the upper second molars have a much lower length to width ratio than is seen in the Terlingua material. Eaton (1987) described similar teeth from the Kaiparowits plateau of southern Utah, arguing that, with the exception of the pitting, the teeth most closely resemble *Cimolodon*. We follow Eaton's conclusions by provisionally referring to the Terlingua material as cf. *Cimolodon*.

Cimolomys clarki Sahni, 1972, is represented in the Terlingua local fauna (Fig. 6) by two upper first molars, one of which is fragmentary. It is significant that *C. clarki* is known exclusively from Judithian faunas (Lillegraven and McKenna, 1986); this occurrence supports the more compelling marine invertebrate data (see below) which indicate the Terlingua local fauna is of Judithian "age."

Two additional multituberculate taxa occur in the Terlingua local fauna. One is based on two upper first molars that are small, with low length to width ratios, and that have distinctive, square-based pyramidal cusps. These features indicate a new taxon endemic to the Terlingua local fauna, but one whose more general affinities are uncertain. For the moment, we refer it to Multituberculata incertae cedis, sp. nov.

The last multituberculate is based on a number of tiny second molars. These teeth closely resemble *Mesodma*, *Cimexomys*, and *Paracimexomys*, but second molars alone do not permit discrimination among these taxa. We refer them to an indeterminate position within Neoplagiaulacidae.

Marsupialia: "Peradectidae" — We follow the usage of Reig et al. (1987) in referring generally primitive Cretaceous marsupials to "Peradectidae," thereby permitting Didelphidae, formerly used for this purpose, to be diagnosed on the basis of presumed synapomorphy (Cifelli, 1990a, d). We acknowledge, however, that this practice perpetuates, rather than eliminates, usage of "wastebasket" taxa. Remains of peradectid marsupials are abundant in the assemblage, but sample sizes are currently insufficient to identify or circumscribe any species reliably. Present evidence suggests the presence of two small species, herein placed in *Alphadon*, and at least one large species, probably referable to *Turgidodon* (genera as defined and diagnosed by Cifelli, 1990a).

Alphadon sp. — This taxon, the smaller of the two Aguja species referred to *Alphadon*, is represented by several upper molars (Fig. 6); lower molars have not been positively identified. Morphologically, this species is typical of *Alphadon*. It is distinct in having small, sharp cusps C and D on the stylar shelf and, especially, in being noticeably smaller than other known Cretaceous marsupials. For example, the average anteroposterior length (A-P length as defined by Lillegraven, 1969) for M2 is 1.39 mm; averages for M2 of other small species are: *Iqualadelphis lactea*, 1.70; *Alphadon wilsoni*, 2.1; and *A. attaragos*, 1.83 (data from Cifelli, 1990a and Lillegraven, 1969).

Alphadon cf. *A. wilsoni* — This species is the most abundant therian in the fauna. It is closely comparable to *Alphadon wilsoni* Lillegraven, 1969, and especially resembles that species in that stylar cusp C is well-defined and conical (Fig. 6). However, the Aguja material is slightly more than one standard deviation smaller than *Alphadon wilsoni* (cf. Lillegraven, 1969: 36–37), suggesting that it may prove to be a distinct taxon as our sample improves.

Turgididon sp. — A third peradectid taxon, currently known only from molar fragments, indicates an unidentified species of *Turgidodon*, identified by large size and by robust, inflated tooth cusps and heavy wear (Cifelli, 1990a). It is approximately the size of the Judithian *Turgidodon russelli* and *T. madseni*, but is insufficiently known to make detailed comparisons.

Pediomyidae: *Pediomys* cf. *P. krejcii* — One small fragment of an upper molar records a tribosphenic therian with a reduced anterior stylar shelf. Recognizing the difficulties involved in interpreting the affinities of such taxa (see Fox, 1987), we refer the species tentatively to *Pediomys*. The species is small, comparable in size to Lancian *P. krejcii* Clemens, 1966; as in that species, cusp D is small and C is apparently lacking.

?Eutheria incertae sedis: *Gallolestes* sp. — This small species (average A-P length for lower molars = 1.44) resembles *Gallolestes pachymandibularis*, from the

Campanian "El Gallo Formation," Baja California (Lillegraven, 1972, 1976). The Aguja species is known by lower molars (Fig. 6); a poorly preserved upper molar may belong to it, but cannot be assigned to *G. pachymandibularis* with confidence. As in *G. pachymandibularis,* the entoconid is placed lingually and the paraconid is low and placed well anterior and labial to the metaconid. In addition to its smaller size, the Aguja species is distinct in having less robust molars, less height differential between protoconid and metaconid, and a deeper labial ectoflexid dividing the trigonid and talonid. An upper molar lacking most of the enamel possibly belongs to this species, based on size (upper molars of *Gallolestes* are otherwise unknown) and its dissimilarity to other tribosphenic therians from the fauna (i.e., it does not belong to a marsupial and appears to be too small for the metatherian-eutherian grade taxon noted above). The stylar shelf, which appears to have lacked cusps in the C to D positions, is modestly developed, except that an enormous parastyle is present, giving the tooth the appearance of an ultimate upper molar. The metacone is well-developed, a point of difference from ultimate upper molars of marsupials and certain Late Cretaceous eutherians, such as *Cimolestes.* The tooth most resembles ultimate upper molars of other Eutheria, such as *Procerberus formicarum;* however, it may be a penultimate molar of a more primitive taxon (cf. Fox, 1975).

The affinities of *Gallolestes* are problematic. Lillegraven (1976) referred the genus to Eutheria, but Clemens (1980), more conservatively, considered it simply as Theria incertae sedis (see also Clemens and Lillegraven, 1986). More recently, Nessov (1985) returned *Gallolestes* to Eutheria, placing it in the otherwise Asiatic suborder Mixotheridia. However, the trigonid configuration does not resemble that of any other Cretaceous mammal, although the reduction of the paraconid is suggestive of Eutheria. Evidence provided by the Aguja materials is inconclusive; if the upper molar is correctly referred and if it represents M3, there is some suggestion of relationship to Late Cretaceous Eutheria.

In summary, the Terlingua mammals include at least one strictly Judithian element, *Cimolomys clarki* (Fox, 1971; Lillegraven and McKenna, 1986), and the remaining taxa are all consistent with a Judithian assignment.

SUMMARY OF AGUJA VERTEBRATES

Table 1 is an uncritical listing of all taxa reported from the Aguja Formation by previous researchers (with citations) and from the Terlingua local fauna. The Aguja Formation includes marine, terrestrial, and intermediate deposits. It appears to span a considerable length of time, including most of the Campanian and perhaps the early part of the Maastrichtian (see below). This list mixes taxa that may have been separated by several million years and that lived in different environments. Table 1 should thus be viewed more as an entrant into the literature on Aguja vertebrate paleontology than as a verified tabulation of the Aguja biota.

DISCUSSION

Age of the Terlingua Local Fauna

Because radiometric dates have not been reported from the Upper Cretaceous section in the Big Bend region, dating of these deposits rests entirely on correlation of the vertebrate and invertebrate faunas, and on limited paleomagnetic stratigraphy. The Big Bend region is uniquely situated between the Cretaceous Western Interior and Gulf Coast marine zoogeographic provinces, and allows correlation of the biostratigraphic zonations developed for each province. Marine invertebrates from the intergonguing Pen and Aguja formations provide a lower limit on the age of the Terlingua local fauna assemblage; continental vertebrates from the overlying Javelina Formation provide an upper limit.

The main body of the Pen Formation lies within the lower Campanian *Delawarella delawarensis* zone, based on the occurrence of this Gulf Coast and Tethyan zonal ammonite, as well as *Menabites belli, Submortoniceras vanuxemi, S. mariscalense,* and *S. chicosense* (Young, 1963). The upper part of the Pen Formation may extend into the overlying *Delawarella sabinalensis* zone, based on a single occurrence of this ammonite (Young, 1963). However, the most common ammonite in the Pen Formation, and in the paralic basal sandstone member of the Aguja Formation, is *Placenticeras syrtale,* known elsewhere from the lower Campanian of both the Gulf Coast and the Western Interior. *Placenticeras meeki* also occurs in the Pen Formation, the McKinney Springs tongue of the Pen Formation, and all sandstone members of the Aguja Formation, but this is a wide-ranging species known elsewhere from throughout the Campanian and Maastrichtian (e.g., Reeside, 1927). The lower Campanian Gulf Coast ammonite *Parapuzosia paulsoni* occurs in the Rattlesnake Mountain sandstone member of the Aguja Formation. Several fragments of *Hoplitoplacenticeras* sp. are now known from the Terlingua Creek sandstone and, more importantly, poorly preserved specimens of *Baculites maclearni* are known from all sandstone members of the Aguja Formation. *Baculites maclearni* is a zonal index for the base of the upper Campanian in the Western Interior (Kauffman, 1977), and is the highest ammonite zone recorded in the Aguja. Lillegraven and Ostresh (1990) recently placed the Aguja above the *Baculites gregoryensis* zone (their Zone 16), whereas the data available to us indicate it to lie no higher than the *Baculites maclearni* zone (zone 11). Collectively, the ammonites indicate that the Pen Formation and the lower part of the Aguja Formation, up to and including the Terlingua Creek sandstone member, are Campanian in age. The lower/upper Campanian boundary probably lies at or above the level of the Rattlesnake Mountain sandstone member.

Gryphaeid, ostreid, and inoceramid bivalves provide a useful supplement to the correlation based on ammonite zonation. *Exogyra ponderosa ponderosa* is abundant in the main body of the Pen Formation and in the lower part of the McKinney Springs tongue of the Pen Formation. In the Gulf Coast, *E. ponderosa ponderosa* is known from lower and upper Campanian strata, up to the zone of *Hoplitoplacenticeras vari* (Young, 1963). *Exogyra ponderosa upatoiensis* is also known from the main body of the Pen Formation; it is not known to occur elsewhere above the zone of *Delawarella delawarensis* (Young, 1963). *E. ponderosa erraticostata* also occurs throughout the Pen Formation, but it is a temporally wide-ranging subspecies. The oysters, *Flemingostrea pratti* and *F. subspatulata*, are abundant in the Rattlesnake Mountain sandstone member of the Aguja Formation, and also occur in the Terlingua Creek sandstone member. *Flemingostrea pratti* is known from upper Campanian, and *F. subspatulata* from upper Campanian and lower Maastrichtian, strata of the Gulf and Atlantic coasts (Wolleben, 1977; Sohl and Christopher, 1983). The oyster *Crassostrea cusseta* is locally abundant in the basal sandstone and Rattlesnake Mountain sandstone members; this species is known elsewhere only from middle Campanian strata of the Gulf Coast (Sohl and Kauffman, 1964). *Inoceramus vanuxemi, I. barabini,* and *I. oblongus* occur abundantly in the McKinney Springs tongue of the Pen Formation, suggesting an early late Campanian age for these strata. Hence, oyster and inoceramid faunas also indicate a Campanian age for the Pen and for the lower, marine part of the Aguja formation, with the lower/upper Campanian boundary falling perhaps at the level of the Rattlesnake Mountain Sandstone member.

Continental Cretaceous strata above the Terlingua Creek sandstome member of the Aguja Formation must at present be correlated on the basis of their vertebrate faunas. The theropod and mammal assemblages in the Terlingua local fauna suggest a Judithian assignment, and all of the remaining Terlingua taxa are consistent with this position. The dinosaurs *Chasmosaurus, Kritosaurus, Panoplosaurus,* and ?*Stegoceras* are known by specimens from higher levels in the upper shale member, and also suggest a Judithian or "Edmontonian" age for these beds (Lehman, 1989). The overlying Javelina Formation bears dinosaurs (*Alamosaurus, Torosaurus, Tyrannosaurus*) and mammals considered to be Lancian (middle to late Maastrichtian) in age (Lawson, 1976; Standhardt, 1986; Lehman, 1990b). Limited paleomagnetic stratigraphy suggests that the base of the Javelina Formation must lie at least as low as polarity chron C30N (mid-Maastrichtian; see Standhardt, 1986; Lehman, 1990b).

In sum, the combined evidence now available suggests that the Terlingua local fauna, which lies at the base of the upper shale member of the Aguja Formation, is late Campanian in age. This fauna appears to be correlative with Judithian Land Mammal "age" faunas known from more northerly parts of the Western Interior, although its composition is considerably different from the typical Judithian faunas upon which the Land Mammal "age" was established. It is also likely that the Aguja Formation as a whole records a considerable expanse of time, and that the Aguja section lying stratigraphically above the Terlingua locality may span Judithian through the beginning of Lancian time.

Relationship with Other Southern Late Cretaceous Terrestrial Faunas

The Terlingua local fauna is not strictly comparable to any other known Cretaceous local fauna, though it does include elements known elsewhere from the Western Interior. Comparison of the Aguja microvertebrate locality with faunas of the Fruitland-Kirtland formations of the San Juan Basin are problematic, in part because the age of the Fruitland-Kirtland formations has been controversial, and in part because their fauna is different in many regards from the classic northern faunas. Like the Aguja Formation, the Fruitland-Kirtland formations probably span a considerable expanse of time. Most recent authors concluded that the Fruitland-Kirtland faunas are of "Edmontonian" age (Lillegraven and Ostresh, 1990; see also Clemens, 1973; Clemens et al., 1979; and Lillegraven and McKenna, 1986; Kequin and Fox, 1991), but data from ammonite stratigraphy and radiometric dates suggest that the best-known mammal faunas, those from the Hunter Wash and Fossil Forest localities, are Judithian, even though they do not resemble the typical northern Judithian assemblages. These localities lie along the southwestern edge of the San Juan Basin, in the stratigraphically lowest part of the Fruitland-Kirtland Formations. Overlying the localities is a well-dated ash bed that yields an age of 72 to 75 Ma (Brookins and Rigby, 1987), which is about the age of the *Didymoceras cheyennense* zone. The highest ammonite beneath the localities is *Baculites scotti,* known from the underlying Pictured Cliffs Sandstone. Hence, the Hunter Wash and Fossil Forest mammal faunas are bracketed between the *B. scotti* and *D. cheyennense* zones, which are equivalent in age to the Judithian faunas of Montana and Canada (e.g., Goodwin and Deino, 1989); stratigraphically higher parts of the Fruitland-Kirtland formations probably extend into the "Edmontonian" and perhaps also Lancian. These conclusions are further supported by Flynn's (1986) comparison of the Hunter Wash mammals with northern Late Cretaceous assemblages. Flynn noted that no Lancian species is present in the Hunter Wash fauna, and that the latter's closest resemblance is to the Pre-Lancian Judith River and Milk River assemblages that define the Judithian "age."

If our preliminary identifications of mammals bear up under more detailed comparisons, the Terlingua and Hunter Wash/Fossil Forest local faunas share *Alphadon* cf. *wilsoni* and *Cimolodon* cf. *electus* (Flynn, 1986); the former taxon is also reported in the Fossil Forest local fauna (Rigby and Wolberg, 1987). Both

taxa occur in northern faunas (Sahni, 1972; Fox 1971); their occurrence in the Terlingua local fauna is southern range extension.

Apart from ceratopsians, which are different in the two faunas, the archosaurian components are not well known in either case. Several ceratopsians are tentatively reported in older literature from the Fruitland-Kirtland formations, but all identifiable specimens recovered from the Hunter Wash-Fossil Forest stratigraphic interval are referable to *Pentaceratops sternbergii* (Rowe et al., 1981; Lehman, 1990a). Its close relative, *Chasmosaurus mariscalensis,* is the only diagnosable ceratopsian yet recognized in the Aguja (Lehman, 1982, 1989, 1990a) and is probably the ceratopsian represented in the Terlingua local fauna. The remaining vertebrates of the New Mexican faunas are too poorly known to afford informative comparisons.

The best represented Late Cretaceous fauna from the southern part of the Western Interior is that of the Kaiparowits Formation, southern Utah, whose mammals are now becoming well-known (Eaton, 1987; Eaton and Cifelli, 1988; Cifelli, 1990a, b, c, d, e). The Kaiparowits assemblages, distributed through 350 m of section, span a considerable period of time and, although quite distinct from more northerly local faunas, almost certainly include part or perhaps all of the Judithian. The Terlingua fauna shares with the Kaiparowits assemblages a new multituberculate taxon, which we referred to above as cf. *Cimolodon,* following Eaton's (1987) suggestion for the Kaiparowits material. No other mammalian species have yet been recognized that are shared by the Kaiparowits and Terlingua faunas, but this will bear reassessment as the faunas are more thoroughly studied. The non-mammalian vertebrates are not yet adequately studied to afford informative comparisons.

The "El Gallo Formation" of Baja California produced the only other Late Campanian non-marine fauna known at present (Morris, 1973; Lillegraven, 1972, 1976; Clemens et al., 1979). In the "El Gallo" fauna is the only other occurrence of *Gallolestes.* The "El Gallo" and Terlingua faunas also share the wide ranging taxa *Pediomys* and possibly *Mesodma,* but neither taxon is adequately known in these southern faunas to permit more specific comparisons. Absent from the Terlingua fauna are polyglyphanodontine squamates, which occur in the "El Gallo" and many northern localities (Estes, 1983a).

Campanian Faunal Differentiation

The composition of the Terlingua local fauna corroborates previous suggestions that latitudinal biotic differentiation developed along the Interior Seaway, and that a biogeographically distinct southern terrestrial fauna existed during the Campanian (Clemens, 1973; Clemens et al., 1979; Flynn, 1986; Eaton, 1987; Lehman, 1987; Wolfe and Upchurch, 1987; Lillegraven and Ostresh, 1990). This is not surprising in light of ample evidence of a distinct southern marine biota

at this time in the Western Interior Seaway (e.g., Sohl, 1971; Kauffman, 1977, 1984; Nicholls and Russell, 1990).

Among mammals, the ?eutherian *Gallolestes* is known only in the two southern-most localities. The distinctive multituberculate that we refer to as cf. *Cimolodon,* which is present in the Terlingua and Kaiparowits faunas (Eaton 1987), has not been found anywhere north of the Kaiparowits Plateau. In this context, it is also notable that pediomyid marsupials are rare and stagodontids appear to be absent in the Terlingua fauna, as is the case with other southern faunas (e.g., Clemens, 1973; Eaton and Cifelli, 1988). Further demarcating southern from northern faunas are endemic multituberculate and marsupial species, which occur in all of the southern faunas except the poorly known "El Gallo."

The Terlingua reptiles also show differences from northern faunas. Four new, endemic squamate taxa occur in the Terlingua fauna, and the only known Campanian snakes occur in the Terlingua and Fruitland-Kirtland faunas. Among archosauromorphs, the ceratopsians of southern faunas are also distinct from northern faunas. *Pentaceratops sternbergii* (Rowe et al., 1981) and *Chasmosaurus mariscalensis* (Lehman, 1982, 1989, 1990a) are endemic to the Fruitland-Kirtland and Terlingua faunas, respectively. Notably absent from the archosauromorph component of the Terlingua fauna, and from the Aguja in general, are champsosaurs. They are reported in the San Juan Basin (Wolberg and LeMone, 1979) and are abundant in more northern faunas (Estes, 1964; Langston, 1975, 1976; Brinkman, 1990).

Collectively, the vertebrates of the Terlingua local fauna indicate an appreciable degree of latitudinal differentiation among contemporaneous faunas bordering the Cretaceous interior seaway. The full significance of Late Cretaceous faunal differentiation will become clear only after the faunas become known in greater detail.

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APPENDIX 1

Voucher specimens for taxa from the Terlingua local fauna mentioned in the text.

CHONDRICHTHYES: *Hybodus* sp. TMM 43057-289, TMM 43057-293, TMM 43057-321; Hybodontidae, indet. TMM 43057-290, TMM 43057-291; *Lissodus selachos* TMM 43057-294, TMM 43057-302; *Scapanorhynchys* sp. TMM 43057-301; *Onchopristis dunklei* TMM 43057-295, TMM 43057-305; *Ischyrhiza avonicola* TMM 43057-292, TMM 43057-306; *Squatirhina americana* TMM 43057-297, TMM 43057-298; *Ptychotrygon* sp. TMM 43057-300, TMM 43057-304; Batomorphii indet. TMM 43057-307; Dasyatidae indet. TMM 43057-296; Chondrichthyes indet. TMM 43057-303.

ACTINOPTERYGII: Leipsosteidae TMM 43057-34, TMM 43057-242, TMM 43057-243, TMM 43057-245; Amiidae TMM 43057-246; Phyllodontidae TMM 43057-244.

LISSAMPHIBIA: *Albanerpeton* cf. *A. nexosus* TMM 43057-247, TMM 43057-249, TMM 43057-250, TMM 43057-251, TMM 43057-252, TMM 43057-253, TMM 43057-254, TMM 43057-255, TMM 43057-257, TMM

43057-258; Prosirinidae sp. TMM 43057-259; Scapherpetontidae TMM 43057-248; Urodela indet. TMM 43057-237, TMM 43057-239; Anura indet. TMM 43057-238, TMM 43057-256, TMM 43057-310, TMM 43057-311, OMNH 25293, OMNH 25305.

CHELONIA: Baenidae OMNH 23143; "*Aspideretes*" TMM 43057-324; isolated dentaries: TMM 43057-129; TMM 43057-130; TMM 43057-131; TMM 43057-132; TMM 43057-133.

SQUAMATA: *Odaxosaurus* sp. TMM 43057-278, TMM 43057-279, TMM 43057-280, OMNH 25226; *Proxestops* sp. TMM 43057-138; Glyptosaurinae indet. TMM 43057-281, TMM 43057-282, TMM 43057-283, OMNH 22981, OMNH 25232, OMNH 25251; *Restes* sp. OMNH 25337; Anguidae indet. OMNH 23035 (in part), OMNH 23038 (in part), OMNH 23035; Necrosauridae indet. TMM 43057-266, OMNH 25222, OMNH 25334; *Sauriscus* sp. TMM 43057-284, TMM 43057-285, OMNH 25336, OMNH 25339, OMNH 25341, OMNH 25347; Scincidae sp. A TMM 43057-286, TMM 43057-287, TMM 43057-288, OMNH 23034, OMNH 23039, OMNH 25223,

OMNH 25225, OMNH 25227, OMNH 25242; Teiidae sp. B TMM 43057-274, TMM 43057-275, TMM 43057-276, OMNH 23037, OMNH 25339, OMNH 25342, OMNH 25343; Squamata indet. sp. X TMM 43057-261, TMM 43057-263, TMM 43057-264, TMM 43057-265, TMM 43057-273, OMNH 25224; Squamata indet. sp. Y TMM 43057-267, TMM 43057-268, TMM 43057-269, TMM 43057-270, TMM 43057-271, OMNH 22982, OMNH 23040; Serpentes TMM 43057-322.

ARCHOSAURIA: Goniopholidae indet. TMM 43057-6; *Deinosuchus* TMM 43057-20, TMM 43057-147; Pterosauria TMM 43057-13; Ankylosauria TMM 43057-136; Hadrosauridae TMM 43057-145; TMM 43057-146; TMM 43057-152; Ceratopsidae TMM 43057-32; cf. *Troodon* TMM 43057-323; cf. *Ricardoestesia* TMM 43057-313; cf. *Dromaeosaurus* TMM 43057-314; cf. *Saurornitholestes* TMM 43057-316, 43057-317.

MAMMALIA: *Meniscoessus,* sp. nov. TMM 43057-62, 43057-63, 43057-64, OMNH 22667, 25089; *Cimolodon* cf. *electus* OMNH 22658, 22661, 22692, 25038, 25041, 25005, 25006, 25042; cf. *Cimolodon* 22670, 22673, 23031, 23032, 25035, 25088; *Cimolomys clarki* OMNH 22682, 25014; Multituberculata, incertae sedis sp. nov. OMNH 22683, 25019. *Alphadon* cf. *A. wilsoni* OMNH 25217; *Alphadon,* sp. OMNH 22721; *Turgidodon* sp. TMM 43057-82; *Pediomys* sp. cf. *P. krejcii* OMNH 22748; *Gallolestes* sp. OMNH 22788; Mammalia, incertae sedis ("metatherian-eutherian grade" or "Tribotheria") OMNH 22786.